

ON THE BIOLOGY AND ECONOMIC SIGNIFICANCE OF *TIPULA PALUDOSA*.

By JOHN RENNIE, D.Sc., F.R.S.E.

(*North of Scotland College of Agriculture.*)

PART I. MATING AND OVIPOSITION.

(With Plate XXXVI.)

IN the course of the summers of 1913 and 1914 the mating and oviposition of *Tipula paludosa* formed the subject of special study both in the field and in laboratory experiments. As far as the writer knows no account of the sexual behaviour of this species is on record, at all events in detail. The points of special interest which have been made out are summarised in the present paper; the observations of the first season have been confirmed in the second.

Mating.

The earliest occasion in a season upon which mating was observed in progress was 20th June, 1914. This was in a field cage in which the flies had hatched out naturally. In the previous year, when a closer watch was kept, and the flies were reared in captivity and probably hatched earlier than in the field, the date was actually later, viz. 4th July. It may here be mentioned that, as detailed in a subsequent paper, there is only one generation of this species in the year in the north of Scotland. In the south of Britain it is held that two generations occur.

The flies experimented with were reared from larvae which had been kept in field and laboratory cages. The pupae were collected and transferred to small vessels about the size of ordinary flower pots

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containing soil covered with small pieces of turf. On the top of the turf was placed a glass cylinder about 9 inches high and $3\frac{1}{2}$ inches in diameter. In some instances, lamp chimneys with nearly twice this width at their base were used. These were about 12 inches high but narrowed to about 2 inches diameter at the top. The vessel was kept closed by a piece of light cardboard placed upon the opening at the top. There were never more than two or three adult insects confined in these simple cages; they appeared quite comfortable and lived in most instances about a week, in some cases as long as eleven days.

The following observations are typical of the general results obtained and will serve as descriptive of the mating habits of these insects under the conditions which have been specified.

On the 5th of July, 1913 at 11.15 a.m. a pair of crane flies of the species *T. paludosa*, here referred to as *M* 1 and *F* 1, was found *in coitu* in one of the larvae rearing cages. They were removed without being separated to one of the glass observation vessels and watched until 1 p.m. at which time they still remained united. At 1.45 p.m. they were found to have separated. They were the sole occupants of this particular cage. This is referred to as Mating (*M*1 + *F*1)1.

At 2.30 p.m. on the same day they again spontaneously effected coitus, remaining attached until 3.30 p.m. Mating (*M*1 + *F*1)2.

At 4.15 p.m. on the same day mating was again accomplished between this pair. Coitus lasted until 5.23 p.m. Mating (*M*1 + *F*1)3.

The same evening these flies were placed together upon a small enclosed grass plot. For a short time they remained indifferent to each other, and the female commenced oviposition.

A second female, *F* 2, newly hatched, was placed beside them and almost immediately the male flew towards her and, after a short struggle in which some of the legs of the female were broken off, coitus was effected. Mating (*M*1 + *F*2)1.

At 10.20 a.m. on the following day a newly hatched male, *M* 2, was introduced to the vessel beside *F* 1, who had as already noted been ovipositing. Union was immediately effected. At 12 noon they still remained *in coitu*, and at this hour they were taken apart and placed in different vessels. Mating (*M*2 + *F*1)1.

At 12.15 p.m. *M* 1 was once more placed beside *F* 1. At 2.40 they had taken no notice of each other. They were now disturbed and made to fly about the cage. Upon coming into proximity they mated. Mating (*M*1 + *F*1)4.

At 4.30 they were found to have separated. They were left together overnight.

On the morning of the 7th, this female *F* 1 was removed to another vessel beside a male, *M* 5, hatched overnight. He flew at her instantly on her arrival and in a few seconds mating was effected, 9.55 a.m. At 11.20 a.m. they were found to have separated. Mating (*M* 5 + *F* 1) 1.

F 1 was now placed in a small glass vessel over some moist cotton wool. Up till 6.35 oviposition had not taken place under these conditions. At this hour she was placed over soil to see if this would now supply the stimulus. The result was negative. This female, however, was known to have oviposited previously, and at this stage she had lost the full-bodied appearance of the unmated female and was quite slender in form.

On the 9th, *F* 1 was placed with another male, *M* 6, but no union took place. From this date she was kept in the company of a male until she died. This occurred upon the 16th and meantime no further mating had been effected in her case. Reviewing the facts regarding her, it is noted that between the morning of the 5th and the morning of the 7th she mated at least six times, and with three different males. She lived 11 days in captivity.

The male *M* 1, as has already been recorded in the account of the behaviour of *F* 1, mated with her four times in the course of two days. He also mated with another, *F* 2, within a short time of her hatching. This took place at 7.10 p.m. on the 6th July. At 9.15 they were still mated, and on the following morning they were again found *in coitu*.

At 10.35 upon the morning of the 6th this male was introduced to a vessel in which there were already three females and one male. He at once flew amongst these and in a few seconds became coupled to a hitherto unmated female *F* 3. They remained *in coitu* until 12.15 when they separated. Subsequently as recorded for the female, *F* 1, he paired with her at 2.40 p.m. of the same day.

No further opportunities for mating were given to this male until the 9th (four days after he was first found mated), on which day he was placed with a newly hatched female *F* 9 at 11 a.m. They were left together until 3.20 p.m. but coitus did not take place. He mated at least seven times in the course of two days. He died upon the 12th, having lived seven days.

A number of similar experiments were performed and always with consistent results. Recently hatched insects paired most readily, and

most were ready upon opportunity to pair a number of times. The following are additional notes.

F 12 placed in vessel with males, *M* 11, *M* 12, and *M* 13. *M* 11 attempted coitus and failed. *M* 12 succeeded. *M* 12 subsequently mated with *F* 13.

F 16, *F* 17, *F* 18 placed in a vessel containing a crowd of males. The males immediately flew to them and in a few seconds all three females were mated.

F 20 and *M* 17, both hatched on the morning of 18th July. They mated at 10.30 a.m. During the day she oviposited. *F* 21 and *M* 18, hatched later in the day, both mated. *F* 21 had defective wings. These four insects were placed together. Both pairs mated again in the evening. On the following evening *F* 20 mated once more with either *M* 17 or *M* 18. By this time she had become quite slender, and had evidently oviposited freely.

F 25, hatched on 28th July. Placed with *M* 24. Mated and oviposited. On the 30th she was placed with 14 males captured in the open. There was much commotion on her arrival and in a short time one of the males succeeded in mating with her.

F 27, hatched 6th August. Dropped into vessel containing *M* 24, *M* 25, and others. An immediate contest for her took place; mating successful.

F 28. Placed with the foregoing, with same result. The males immediately surrounded her, and mating was effected in the course of a few seconds.

In seeking to effect coitus, the male alights above the female and prevents her escape, should she attempt it, by intermingling of their limbs. Meantime his abdomen, which is now markedly upturned at the tip, is passed below that of his mate. The widely gaping claspers seize her on the thickened basal part of the ovipositor and the hold having been made secure the pair rest a few moments in this position. The male, now releasing his hold by the limbs, turns round so as to face in the opposite direction from the female. This is the position maintained until separation takes place. Sometimes the wings are folded, but more usually in both sexes they are extended. During coitus the antennae of the male continue in active backward and forward quivering motion. In his case too, the halteres quiver periodically in spasms of about a second's duration and at frequent but irregular intervals. This last

feature was constantly to be observed and appeared to be directly associated with the sexual activity in progress. After attachment contractile movements are observable at the tips of both abdomens for a short period; subsequently the female rests absolutely passive. Cf. Plate XXXVI.

Oviposition.

This may take place quite early after mating. *F* 1 after having mated three times upon the 5th July commenced oviposition in the evening. *F* 2 mated on the 5th was watched in the process of egg laying on the morning of the 6th. Another female, *F* 5, hatched at 9.50 a.m. upon the 7th and mated immediately afterwards. She mated again with the same male *M* 12 in the afternoon. They separated at 4.20 and at 5.27 she was watched engaged in oviposition, and her eggs were collected when she had moved away.

Curtis (*Farm Insects*, p. 445) says: "the eggs are laid by the females as they fly or when they rest among the herbage and are propelled as from a pop-gun." So far I have not been able to witness this propulsion of the eggs while the insects were on the wing, but it will be understood that the conditions of my earlier experiments were not favourable to this method.

I have repeatedly watched the process amongst grasses. The female stands in a vertical position with the ovipositor pushed well down and into the soil if she can reach it. Sometimes a backward and forward screwing motion of the body is indulged in so that the ovipositor is bored well into the ground. Spasmodic jerks of the hinder part of the abdomen indicate the expulsion of the eggs one by one. After a few minutes she moves along a little way and the process is repeated. About half-a-dozen eggs may be deposited at the same spot, frequently fewer. In one case I was able on lifting a female, not actually ovipositing but exhibiting spasmodic movements of the ovipositor, to get her to lay an egg upon a card in my hand.

Newly hatched females are bulky in appearance at the anterior end of the abdomen. After oviposition they become slender. In this way one can tell whether a female has oviposited or not, though not generally whether the process is completed or not. The eggs in the newly hatched female mostly show black in colour through the skin and are shelled before fertilization. Advanced female pupae have the abdomen filled with the ovaries which are of a pale salmon pink

colour. Dissection of females some time after oviposition shows that all the ova are not mature at hatching but that there is at least a second batch of eggs. Females captured in the open which are slender bodied, *i.e.* which show signs of having oviposited, have small pear-shaped ovaries occupying the posterior part of the abdominal cavity. The eggs in these may be well-developed and of the typical shape as when mature, but of the pale salmon colour. This suggests that females having oviposited may continue to live and to produce a fresh race of ova. This second lot of ova is not merely mature at hatching but without shells: they increase in size during the adult period. A female, *F* 22, hatched on the evening of the 20th July, and which had been mated and had oviposited, died on the 26th. Dissection showed that all the black shelled ova had been laid, and that the ovaries were small in size and confined to the hinder part of the abdomen. In this case, however, the individual ova were much smaller and had much less yolk than was found in the fly captured in the open and which was therefore presumably older. The question of the length of life of individual crane flies has not so far been settled.

Experiments were performed to test the degree of stimulus needed for the act of oviposition. Flies which had been mated and were placed upon cotton wool did not oviposit. Also when the wool was placed upon a layer of soil, they still failed to respond. Only in a few cases were eggs laid upon bare soil, whilst amongst herbage they were deposited readily. Although crane flies are known to oviposit usually in grass, it was found that they may do so in standing corn also.

The flies kept in captivity were not fed. They usually had access to growing grasses, and to soil, both of which were watered. They were observed licking at moist soil and at the wet sides of the glass vessels in which they were confined.

EXPLANATION OF PLATE XXXVI.

View of *Tipula paludosa* in coitu. The halteres are not visible owing to their vibratory movements.